

Review

Taro Leaf Blight—A Threat to Food Security

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Abstract: Taro leaf blight (caused by the Oomycete *Phytophthora colocasiae*) is a disease of major importance in many regions of the world where taro is grown. Serious outbreaks of taro leaf blight in Samoa in 1993 and in the last few years in Cameroon, Ghana and Nigeria continue to demonstrate the devastating impact of this disease on the livelihoods and food security of small farmers and rural communities dependent on the crop. The spread of the disease to new geographical areas also poses a major threat to neighbouring countries and taro growing regions still free from the disease. Past research, particularly in the Pacific, has demonstrated that management measures such as chemical and cultural control are largely ineffective and that breeding for disease resistance is the most sustainable approach to manage the disease. Recently, the Pacific and South-east Asian regional taro networks have made excellent progress in developing cultivars resistant to taro leaf blight through enhanced utilization of taro genetic resources and close collaboration between farmers and researchers in breeding programs. These programs have

secured vital taro genetic resources for future use. This paper provides an overview of the disease, its origin, distribution, biology, epidemiology, management and global impact. The paper will largely focus on breeding strategies to address the disease including challenges, opportunities and constraints. It also discusses how these breeding experiences and outputs can be scaled up to other geographical areas where the disease has been recently introduced or under threat of introduction.

Keywords: taro; *Colocasia esculenta*; taro leaf blight; *Phytophthora colocasiae*; resistance breeding; networks

1. Introduction

Taro (*Colocasia esculenta*) a clonally propagated aroid, is grown largely in humid tropical areas of the world. The crop, first domesticated in South-east Asia, has continued to spread throughout the world and is now an important crop in Asia, the Pacific, Africa and the Caribbean [1]. It is the most important edible species of the monocotyledonous family Araceae. Almost all parts of a taro plant are utilized; corms are baked, roasted, or boiled as a source of carbohydrates, leaves are frequently consumed as a vegetable representing an important source of vitamins, and even petioles and flowers are consumed in certain parts of the world. Worldwide, taro ranks fourteenth among staple vegetable crops with about 12 million tonnes produced globally from about 2 million hectares with an average yield of 6 t/ha [2]. Most of the global taro production comes from developing countries, characterized by smallholder production systems relying on minimum external resource inputs. This makes this food crop very important for food security, especially among subsistence farmers in developing countries.

Worldwide, it is believed that crop diseases reduce agricultural productivity by more than 10%, equivalent to half a billion tonnes of food every year [3]. The epidemics associated with these diseases reduce food availability, increase food prices and pose a danger to rural livelihoods and regional food security. According to Fisher *et al.* [4] more than 600M people could be fed each year by halting the spread of fungal diseases in the world's five most important crops alone. The overwhelming impact of plant diseases on human societies and food security is well illustrated by the effect of late blight disease of potato, caused by the pathogen *Phytophthora infestans* in Ireland during the 1840s, at a time when potato was an important staple food for the majority of the population. The disease was one of the factors that led to mass starvation, death and migration. There have been numerous other plant disease epidemics throughout agricultural history that have resulted in a major socio-economic impact; for example, the epidemics caused by coffee rust (*Hemileia vastatrix*) in Sri Lanka (1890s), brown spot of rice (*Cochliobolus miyabeanus*) in India (1940s), wheat stem rust (*Puccinia graminis*) in north America (1960s), rubber leaf blight (*Microcyclus ulei*) in Latin America (1910s), and downy mildew of grape (*Plasmopara viticola*) in Europe (1880s) [5].

The important but neglected taro crop is no exception and is subject to significant losses from diseases and pests. Taro is affected by at least 10 major diseases and pests in different parts of the world [6]. Of the various taro diseases, taro leaf blight (TLB) caused by the fungus-like Oomycete *Phytophthora colocasiae* Raciborski (*P. colocasiae*) is of prime importance because it can reduce corm

yield by up to 50% [7–10] and leaf yield by 95% in susceptible varieties [11]. TLB can also deteriorate corm quality [12,13]. In addition to corm yield losses that occur as a consequence of the reduced leaf area [7] in diseased plants, a corm rot caused by *P. colocasiae* may also occur [5]. Under some circumstances the disease invades harvested corms and causes heavy losses during storage [14].

Repeated outbreaks of TLB in the South Pacific, South-east Asia and recently in West Africa have signalled the urgency to find sustainable solutions to the disease. If uncontrolled, TLB poses a grave threat to food security and loss of crop genetic diversity, as well as impact on personal incomes and national economies. The devastation caused to the taro industry in Samoa (previously known as Western Samoa) as a result of the TLB outbreak in the early 1990s is an example of the destructive nature of the disease [15]. The disease caused serious economic hardship in rural areas, food insecurity and the loss of vital export earnings for the country. The introduction of TLB to the Caribbean in 2004 led to the annihilation of the taro crop in the Dominican Republic, Cuba and Puerto Rico [1]. Most recently TLB has been reported from West Africa in Cameroon [16], Nigeria [17] and Ghana [18] where it continues to decimate taro cultivation, and is impacting on the livelihoods and food security of rural communities. A number of other countries in West and Central Africa may face the same problem because the disease has the capacity to spread on taro planting material—the Oomycete has been reported to survive on planting tops for up to 3 weeks after harvest [19].

This paper provides an overview of TLB, its symptoms, origin, distribution, epidemiology, management and global impact. The paper will focus on breeding strategies to address the challenges presented by the disease, and how countries vulnerable to its advance can take advantage of the experiences and outputs of previous initiatives that have had to deal with its devastation.

2. History of Taro Leaf Blight Epidemics and Impacts

There has been limited documentation of the impact of TLB on countries and communities affected by the disease apart from the Pacific region. In most cases, wherever the disease has occurred in the Pacific, for example in Papua New Guinea, Solomon Islands, American Samoa and Samoa, the introduction of TLB has forced growers to abandon taro and grow other root crops [20].

It is believed that TLB has been present in the Pacific region since the early 1900s [21]. The disease was first recorded in Guam (1918) and later in Hawaii (1920). Prior to the arrival of the disease in Hawaii, it was thought that there were more than 300 different taro varieties but only a few have survived the impact of the disease [22]. Similarly, in Guam, more than 60% of known varieties are believed to have been lost as a consequence of the disease [23,24].

In Micronesia, TLB was reported during the Japanese occupation of Pohnpei [5]. Since then it is thought to have contributed to changes in the cropping system, which in turn has affected dietary patterns. Today, cassava has replaced taro as a major staple [25,26]. Most if not all the varieties that existed before the arrival of the Japanese are no longer present [22]. Taro now ranks behind yams, banana, rice, and breadfruit in Pohnpei [27].

In Papua New Guinea, outbreaks of TLB over the years are believed to have led to the decline in taro production and its displacement by sweet potato [28–30]. Most likely, the disease spread there from Indonesia during the Second World War. The outbreak in Bougainville was said to have contributed to the death of at least 3000 people [31]. Possibly, the occurrence of war forced

communities to vacate their villages and take to forests, and the loss of taro to sustain them resulted in hunger and malnutrition [23,32]. More recently, severe epidemics occurred on the island of Manus in 1976 and in Milne Bay in 1988 completely destroying the crop on each occasion [20]. In Solomon Islands, the disease first appeared in the Shortland Islands in 1946 [33] and within a few years it swiftly spread to most provinces. The disease contributed to a decline in taro production throughout the country [5]. As in Papua New Guinea, disease outbreaks led to sweet potato rapidly replacing taro as the staple food crop [34].

The 1993-1994 epidemic of TLB in American Samoa and Samoa was catastrophic for taro production [35]. Before the disease introduction, taro was the main agricultural export of Samoa, but within six months there was little to trade [36]. Production fell from 0.4 million tonnes per year before the epidemic to less than 5 tonnes by the end of 1995 [37]. In 1993, the export value of taro for Samoa was US\$3.5 million (about 58% of Samoa's agricultural exports) but by 1994 the value had declined to less than US\$60,000 [38] or about 0.5% of the 1993 export figure. Within two years from the start of outbreak in the Samoas, only 200 farmers were growing taro; these were farmers who had the resources to purchase fungicides. Most other growers abandoned the crop and shifted to alternative though less preferred crops such as *Alocasia*, *Xanthosoma*, breadfruit, banana, sweet potato and cassava. By 1994, supplies of taro on the local market were only 1% of the supplies of the previous year [39]. In response, both countries increased rice imports resulting in large trade imbalances.

In 2010, TLB spread to the West African nation of Cameroon where it caused harvest losses of up to 90% [16]. Not only are market prices very high for the little that is now available, there is a scarcity of planting material. The future is uncertain, as it is not clear if alternative food crops can fill the gap left by the demise of taro. Maize production in Cameroon has never met demand and plantains are usually very expensive. There is concern for food security and social unrest. The disease has spread rapidly to other countries in West Africa, including Nigeria and Ghana [17,18]. While it is too early to assess the impact of TLB on these countries, experience tells us that the disease has a potential to create a devastating cascade effect: reduction in food and household incomes, increased poverty and even starvation.

3. Diseases Symptoms

As its name implies, the most obvious and frequent symptom is a blight of the leaf lamina, but *P. colocasiae* also produces a postharvest rot of the corms. A petiole rot is also seen in susceptible varieties [37]. Early leaf infections often take place where rainfall, dew, or guttation droplets accumulate. Initial infections form water-soaked lesions that rapidly expand to form large brown spots [11]. The development of these lesions follows a characteristic day/night pattern. During the night, the lesions expand by developing a 3–5 mm wide water-soaked margin. This margin dries out during the day and a newer water-soaked zone forms the following night [40]. This results in a zonate pattern most easily seen when viewed from the bottom of leaf. Masses of sporangia form on the expanding margin of the lesion during the night, imparting a white powdery appearance to the lesions.

A conspicuous and characteristic feature of TLB lesions is the formation of droplets of amber, bright-orange, or reddish-brown exudate, oozing from the upper and lower surface of the water-soaked margins. These droplets dry out during the day to form crusty deposits on the surface of the lesion. It is

common to observe lesions of different stages on the leaf. Lesions are also formed by sporangia that are splashed by irrigation, rain or wind-drive rain. As the lesion gets larger, the dead central area often breaks and falls out.

Infected petioles are uncommon, but occur in susceptible varieties. The infections start as small, brown, elongated spots. In wet weather, the spots can expand and soften until the petioles are broken by the weight of their leaves [41]. During dry weather the rate of lesion expansion generally slows and lesions may change colour, turning tan to brown with dark brown margins. In some resistant taro cultivars, the centre of lesions become papery and break apart, which gives a conspicuous “shot-hole” appearance [11]. Leaves of susceptible varieties collapse in about 20 days compared to 40 days for non-infected plants [42,43]. Therefore, photosynthesis is greatly reduced in susceptible plants, leading to progressively smaller leaves and corms.

Corm rots usually develop rapidly after harvest and entire corms can decay in 7–10 days. The rots usually start from areas damaged at harvest when the petiole bases and suckers are removed, especially during or after wet, warm conditions. In the early stages, the diseased tissue is light-brown, firm, and often has a distinct margin. In the advanced stages of corm rot, the decayed corm tissue may be invaded by *Lasiodiplodia theobromae* and turn black [14].

4. Origin, Dispersal and Distribution of Disease

Taro leaf blight was first described by Raciborski in 1900 [44] who named its causal pathogen *P. colocasiae* Racib. Information on the origin of *P. colocasiae* is limited [45] and the area of origin remains undefined [46]. Trujillo [9] speculated that the pathogen might have originated in South-east Asia, based on earlier reports of the disease in India. Ko [47] supported Asia as the centre of origin of *P. colocasiae* because of the coexistence of wild and cultivated varieties of taro in the region. According to Zentmyer [45], one of the indications of the centre of origin of an organism such as *Phytophthora* is the co-existence of A1 and A2 mating types with roughly an equal distribution in the same area. Based on this hypothesis, Ann *et al.* [48] screened about 800 isolates of *P. colocasiae* from Taiwan and all acted as A2 mating types, indicating that it is most likely not indigenous to Taiwan. Only the A1 mating type was previously reported from India [49] although recently A2 mating types from India have also been reported [50,51]. A further hypothesis of an Asian origin of *P. colocasiae* has recently come from China [46], where previously only A2 mating types were reported [52]. However, analysis of more than 200 isolates of *P. colocasiae* obtained from Hainan Island (an offshore island in the tropical region of southern China) recovered all three mating types, A0, A1 and A2 indicating that Hainan Island is likely to be inside the centre of origin of *P. colocasiae* from where it was dispersed. Fullerton & Tyson [53] reported only A2 mating type from Papua New Guinea, Hawaii and Guam, excluding these countries from the centre of origin of *P. colocasiae*. Tyson & Fullerton [51] further studied mating types of *P. colocasiae* from the Pacific region, South-east Asia and India and detected only A2 types, extending the A2 mating type list further to Indonesia, India, Philippines, Pohnpei, Thailand and Vietnam. Because of the apparently restricted distribution of the A1 mating type and the geographical separation from the areas in which it is found (Hainan Island, China and Northern India), the likelihood of the introduction of the A1 mating type to the Pacific region is considered to be relatively small [51].

Trujillo [9] postulated that the disease spread into the Pacific region by three different routes based on a possible South-east Asian origin for the pathogen. The first dispersal route is to Hawaii via the Philippines, the second from Taiwan to Micronesia via the Philippines and the third to Fiji via Papua New Guinea and Solomon Islands. At that time, TLB was reported to be present in Fiji but that record was based on a misidentification [5,23,40]. Nevertheless, the movement of TLB to Papua New Guinea and Solomon Islands would appear to be a separate route and is supported by only anecdotal evidence that the disease appeared after the Western Pacific Campaign of the Second World War [54]. Ooka [44] hypothesized that movement on the northern route went from Java to Taiwan, where the disease was reported in 1911. From Taiwan, it is believed to have moved to Japan and thence to Hawaii where it arrived in 1920 [21]. The disease was first recorded in the Philippines in 1916 and movement to Micronesia most likely occurred from there considering the disease was first recorded in Guam in 1918 [55]. There have been no studies on the distribution of mating types in American Samoa and Samoa that could indicate the likely sources of the pathogen, although it is widely speculated that the pathogen arrived in Samoa from Hawaii, probably through infected taro planting material [3].

The pathogen is believed to be distributed by means of vegetatively propagated material, and possibly by soil movement. The Oomycete is now widely distributed geographically over almost all continents including Asia (Bangladesh, Brunei, China, India, Indonesia, Irian Jaya, Japan, Korea, Malaysia, Peninsular Malaysia, Myanmar, Nepal, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand), Africa (Cameroon, Equatorial Guinea, Ethiopia, Ghana, Nigeria, Seychelles), North America (USA), Central America and Caribbean (Brazil, Cuba, Dominican Republic, Puerto Rico, Trinidad and Tobago), South America (Argentina), Oceania (American Samoa, Guam, Northern Mariana Islands, Palau, Papua New Guinea, Samoa, Solomon Islands) [17,18,56,57]. Some of these reports have not been verified and need confirmation. For example, the disease in Fiji is clearly an invalid record [40].

5. Biology of the Pathogen

5.1. Host Range

Phytophthora colocasiae has limited host range [11]. The pathogen is known to infect primarily *Colocasia* spp. (*C. esculenta*, *C. esculenta* var. *globulifer*, *C. antiquorum*) and *Alocasia macrorrhiza* (giant taro). Although *Alocasia* taro can be infected by the pathogen, the ability of the disease to become epidemic on this host is restricted by very low inoculum production [5]. *Xanthosoma* spp. (*Xanthosoma sagittifolia*) is immune [40]. Other reported hosts include *Amorphophallus campanulatus* (elephant-foot yam), *Bougainvillea spectabilis* (bougainvillea), *Cantharanthus roseus* (periwinkle), *Dracontium polyphyllum* (guapa), *Hevea brasiliensis* (rubber), *Panax quinquefolius* (American ginseng), *Piper betle* (betel), *Piper nigrum* (black pepper), *Ricinis communis* (castor bean) and *Vinca rosea* (periwinkle) [58]. Many of the records from these hosts, however, need to be confirmed.

5.2. Life Cycle

The disease cycle of *P. colocasiae* is dependent upon environmental factors (rainfall, humidity and temperature) and host genotype. The primary reproductive unit of the pathogen is the sporangium which requires free water to germinate. Although taro leaves have a waxy surface, the tiny droplets of water that accumulate on leaves provide sufficient moisture for sporangia to germinate. Under cooler conditions (close to 20 °C), the cytoplasm within each sporangium differentiates into 15–20 zoospores (Figures 1 and 2), each oozing out through the terminal pore and moving through the water using their flagella. This is a rapid process and from the beginning of differentiation in the cytoplasm to zoospore release takes less than a minute. The zoospores settle onto the leaf surface within 10 min, lose their flagella and form a rounded cyst which soon germinates to form a germ tube. This mode of germination often referred as the “indirect mode” provides a strong ecological advantage to the pathogen as it generates up to a 15-fold increase in inoculum. New infections can be initiated within an hour of a sporangium being formed and *P. colocasiae* can continue sporulating and infecting during short periods of leaf wetness [40]. Under warmer conditions (about 25 °C), the sporangia germinate directly by germ tubes that can infect the leaves (Figure 1). This form of germination generally referred to as the “direct mode” is a slower process than zoospore production as it can take 5–6 h for a sporangium to germinate. The proportion of sporangia germinating directly is usually much lower than for those forming zoospores [59].

Figure 1. Sporangia of *P. colocasiae* germinating directly and also by production of zoospores.

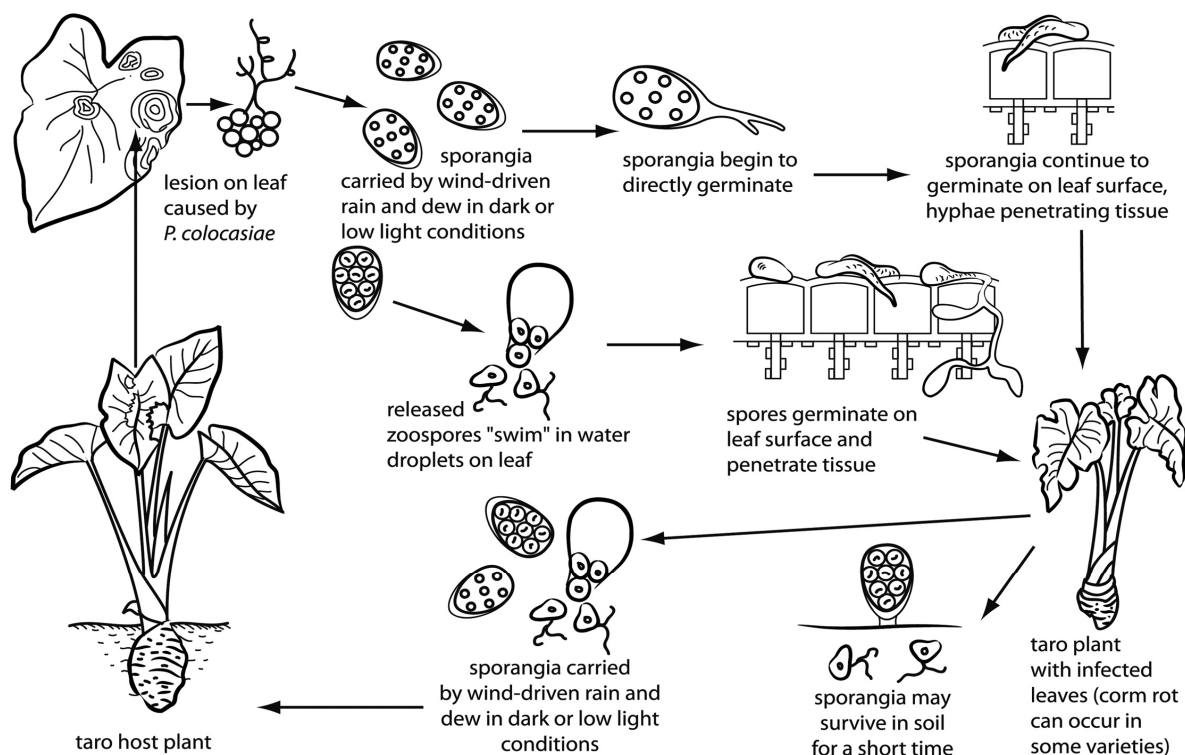
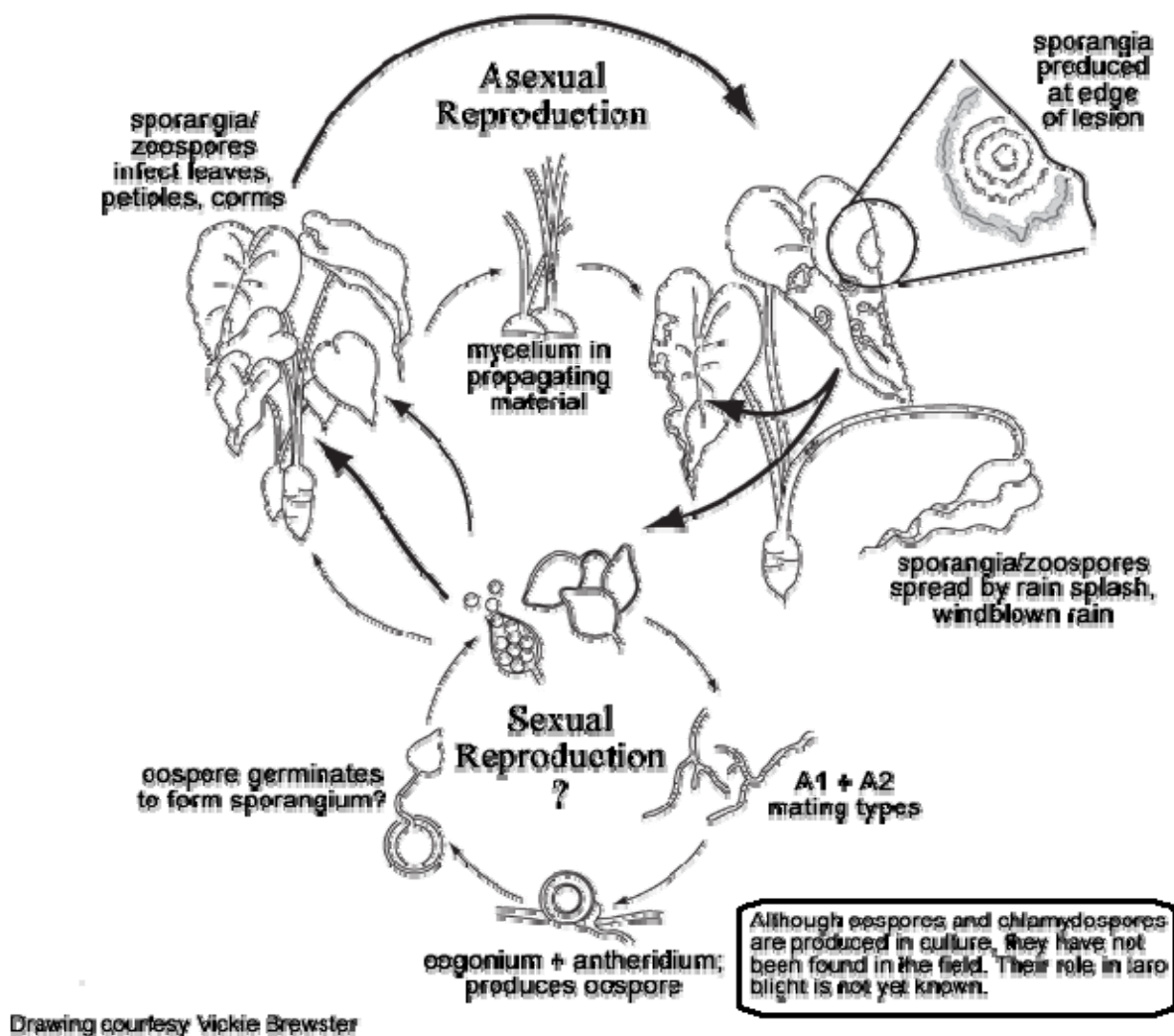


Figure 2. Taro leaf blight disease cycle and epidemiology.

5.3. Infection Process and Conditions

Infection can occur on both surfaces of the leaf [11] and most infections occur between midnight and dawn [59]. Daytime infections occur only during continuously wet conditions. During infection, germ tubes developing from either sporangia or encysted zoospores penetrate the epidermis directly or enter via stomata. After penetration, the Oomycete spreads intercellularly through the mesophyll. First symptoms usually appear within 24 h and the rate of symptom development is greatest at temperatures in the range 25–30 °C under cloudy and/or showery conditions. At 35 °C symptom development is suppressed.

In wetland taro, sporangia can move with the water throughout a field and into adjacent paddies. The pathogen can also live for a time as mycelium in dead and dying plant tissues and in infected corms. During dry periods it can survive in the soil as encysted zoospores, or possibly as chlamydospores [60]. The life span of fungal mycelium in soils is usually short, surviving for less than five days. However, the encysted zoospores of *P. colocasiae* can endure for several months in the

absence of a living host. Most sporangia in vegetative material (e.g., tops used for planting) seldom survive more than a few days though some have been shown to survive for up to 2 weeks [53]. Oospores and chlamydospores may operate as survival structures in infected plant tissues or sometimes in soils, but they are not frequently detected in the field (Figure 2) [11].

5.4. Genetic Variability and Heterothallism

P. colocasiae is a diploid heterothallic Oomycete, requiring opposite mating types (A1 and A2) for the formation of oospores [51]. Heterothallic species of *Phytophthora* readily produce oospores in pairings (intra- or inter-specific) of two compatible mating types [47] and different strains are likely to recombine and evolve rapidly depending on the frequency of A1 and A2 mating types. While oospore formation can be readily induced between opposite mating types in culture, there is no evidence that this event occurs regularly in nature.

The extent of genetic variability in *P. colocasiae* is unknown but in other *Phytophthora* species, sexual reproduction is associated with increased genetic variation, including increased variability in virulence and aggressiveness [53]. The capacity for sexual reproduction in *P. colocasiae* [46,49] has already been documented. Recently, Lebot *et al.* [61] studied isozyme variation among isolates of *P. colocasiae* originating from South-east Asia and the Pacific region and the results indicated that throughout this vast geographic region, TLB is caused by a plethora of distinct and genetically variable isolates. Variations occur within and among countries. Because *P. colocasiae* is diploid and heterothallic, different genetically variable isolates are likely to recombine and evolve depending on the frequency and occurrence of A1 and A2 mating types. Lebot *et al.* [61] have demonstrated that all zymotypes are unique to each country and this might be an indication of rapid evolution within isolated populations. In some countries, for example, Thailand, the high level of genetic diversity might indicate that both migration and sexual recombination play important roles in the population dynamics of *P. colocasiae*. However, Fullerton and Tyson [53] argued that although pathogenic variability may be inferred from a high degree of variability determined by enzyme or molecular analysis, this has not yet been demonstrated.

6. Disease Epidemiology

Favourable temperatures and regular periods of leaf wetness, particularly in the humid tropics promote TLB epidemics by favouring pathogen dispersal, infection, and disease development [62]. Outbreaks of the disease in new areas distant from known centres of infection probably result from the introduction of infected planting material. Within an infected area, the first lesions are due to infection from adjacent plants. Epidemics generally flourish when night temperatures are in the range 17–20 °C. The cool temperatures stimulate the release of infective zoospores, promoting multiple infections.

Taro leaves have waxy hydrophobic leaf cuticles, which assist the wash-off of sporangia and zoospores from the leaves into soil, or their splash onto other leaves and petioles, particularly the lower older ones. However, in the absence of regular rainfall, conditions favourable to re-infection occur on most nights ensuring regular cycling and survival on infected plants thus making it endemic. Under conditions of endemic survival, the distribution of infected plants in an area, and the severity of symptoms on those plants are generally irregular; while some plants become severely diseased with

continuous night time sporulation and localised re-infection, others immediately adjacent may have little or no disease [53]. Generally, older leaves or younger leaves lower in the canopy are most severely affected because of a number of factors: a constant supply of inoculum deposited by runoff water or dew from above; a more conducive microclimate for the Oomycete lower in the canopy; and also because the less waxy cuticles of older leaves tolerates better adhesion of spore-carrying water drops [53]. Under normal circumstances large numbers of sporangia are also washed from lower leaves into the soil. While most of these lyse within the first few days, a small proportion develops thick walls, forming chlamydospores that are able to survive in soil for up to three months [60]. The importance of soil borne chlamydospores in the epidemiology of the disease has not been established but they could allow survival of the pathogen between crops [53]. In situations where vegetative material dies off because of drought or cold conditions, the pathogen most likely survives between seasons as vegetative mycelium in the infected corms [63]. In wetland taro production, the movement of paddy water carries these sporangia and zoospores among plants and between fields. Because growers propagate taro vegetatively, they often unknowingly transport *P. colocasiae* between fields and over long distances by the movement of infected planting material [11].

7. Disease Management Strategies

7.1. Cultural and Biological Control

A number of cultural methods have been recommended for the control of TLB disease. Individually each may be of limited benefit, but collectively they may play an important role in an integrated approach to disease management. The main cultural practices include removal of infected leaves during the early stages of disease development, wide spacing of plants to reduce disease spread, selection of sites surrounded by forest as a barrier to disease spread, isolation of new crops from those that are diseased, and the use of planting material free from disease [11,23,43]. Putter [59] showed that the removal of infected leaves was highly effective in controlling the disease in subsistence taro gardens, particularly when plots were relatively well separated from one another. This strategy can be effective when the disease is in an endemic phase with a relatively low and restricted disease incidence. In contrast, when the disease is in an epidemic phase, the removal of all leaves with lesions may lead to almost complete defoliation of the crop with consequent effects on yield [43]. This was the experience of growers in Samoa [64] where sanitation was largely abandoned as a disease management strategy. In some situations, intercropping of taro with other crops may help in reducing disease. Disease severity was found to be consistently higher in taro monocrops than in a taro/maize intercropping system [23,65]. Foliar application of biological control agents has some potential to protect taro crops from infection. For example, significant reductions in the numbers of infected leaves and disease severity were observed in taro plants sprayed with the fungus *Trichoderma* [66]. In Phichit plain near Phitsanulok, Thailand, some professional taro growers avoid serious TLB infections by planting during the dry season (V. Lebot, personal communication 2012) [67].

7.2. Chemical Control

Successful control of TLB is possible with chemicals even in high rainfall areas. A range of protectant and systemic fungicides have been found to provide effective control of TLB [7,11,43]. Mancozeb (e.g., Dithane M45), copper (e.g., copper oxychloride), metalaxyl (e.g., Ridomil Gold MZ) and phosphorus acid (e.g., Foschek) are amongst those most commonly recommended. Mancozeb and copper have protectant activity only. Metalaxyl and phosphorus acid are generally specific for *Phytophthora* diseases with the former prone to the development of resistance by the organism [53]. In contrast Jackson *et al.* [43] found that Mancozeb did not control the disease in Solomon Islands suggesting that results with chemical control can be variable. Similarly, Trujillo [68] reported that copper gave little control in Hawaii. In Samoa, a research program to investigate chemical control [3] recommended that phosphorus acid (Foschek), which was shown to give good control of TLB, should be alternated with Mancozeb to reduce costs and minimise the possibility of the Oomycete developing resistance. It was also observed that there were no significant differences between phosphorus acid formulations (Foschek, Agri-Fos 400 and Foli-R-Fos) for disease control. In some cases, soils may be drenched with approved products such as MetaStar or Ridomil as a pre-plant treatment and provide initial protection against TLB for 4–6 weeks [11].

The efficacy of fungicides is strongly governed by the severity of the disease at the time, and the prevailing weather conditions [53]. Generally, fungicides are most effective when disease incidence is low and timely applications reduce inoculum levels. When diseases enter an exponential phase, efficacy of disease control is reduced. Efficacy is also influenced by method of application, with motorised knapsack applications superior to conventional hydraulic machines [7,43], a fact related to improved coverage and speed of application especially in high rainfall situations. However, for most situations, the use of fungicides however applied is neither economically sustainable nor environmentally suitable.

7.3. Resistant Cultivars and Genetic Resources

The use of resistant varieties offers the most sustainable management strategy against TLB in most production systems. Resistance can be classified as either vertical or horizontal. Vertical resistance (VR), also referred to as monogenic resistance is generally controlled by one or few major genes and provides complete control against certain races of a pathogen [69]. It is often characterized by a hypersensitive reaction in the host. In a number of cases a gene-for-gene relationship has been demonstrated [70]. Subsequently, new pathogen races evolve that are able to attack previously resistant plants. For this reason, VR is often referred to as non-durable resistance [71].

The genetic control of VR against TLB may not be very complicated and simply inherited [72]. Although a number of genotypes have been shown to express a hypersensitive reaction when challenged by *P. colocasiae*, to date there is no evidence of breakdown of resistance by matching pathotypes [53]. However, it is an area little investigated. In contrast, horizontal resistance (HR) is controlled by a number of minor genes and does not involve a gene-for-gene relationship. It is considered effective against all races of a pathogen and has a reputation for durability, hence referred to as durable resistance. Unlike VR, this type of resistance does not give complete control but limits

the spread of the pathogen within the plant and frequently reduces sporulation. The resistance mechanism in taro against TLB is considered to fall under the HR category based on several host-pathogen interaction models and genetic studies [69,70,73]. Because of predominant heterozygosity of taro genotypes, it is not easy to study the inheritance in a classical Mendelian fashion [74].

The physiological and biochemical mechanisms of resistance and host defence responses have not been studied in detail in the taro and *P. colocasiae* pathosystem [75]. Characteristic defence response in taro like many other host species likely includes systemic events through signalling and possibly constitutive and hydrolytic enzymes, enzyme inhibitors and phytoalexins. It was, however, established by Ho and Ramsden [75] that peroxidase enzymes play no vital role in the defence mechanisms of taro and proteinase inhibitors were the most important components for resistance to TLB. Recently Sharma *et al.* [76] employed suppressive subtractive hybridization, cDNA libraries, Northern blot analysis, high throughput DNA sequencing, and bioinformatics to identify the defence-related genes in taro induced by *P. colocasiae* infection. Using these genomic tools, two putative resistance genes and a transcription factor among the upregulated sequences were identified. There was a higher overall expression of these genes in TLB-resistant genotypes than in those susceptible to the disease.

Resistance in the majority of taro germplasm worldwide was previously considered to be limited globally. Recent evaluations, however, indicate that resistance in traditional cultivars exists in germplasm collections of several countries where TLB has been present for a long time, including the Philippines, Vietnam, Thailand, Malaysia, Indonesia and India [74]. Over twenty TLB-resistant taro varieties were also identified in germplasm from Palau. These genotypes also performed well in field trials in Hawaii [77,78] and many other Pacific Island countries. The genetic diversity of available resistance is, however, considered to be limited although germplasm from South-east Asia is considered to be more diverse than that in the Pacific [79–81]. The Centre for Pacific Crops and Trees (CePaCT formerly the Regional Germplasm Centre (RGC)) of the Secretariat of Pacific Community (SPC) maintains a collection of taro varieties with varying levels resistance to TLB. These varieties are the products of breeding programs in Hawaii, Papua New Guinea and Samoa. The CePaCT also has taro varieties from Asia, which have shown TLB resistance when evaluated in their countries of origin. In Hawaii, a new program collected almost 300 taro genotypes from Nepal, Thailand, Vietnam, Indonesia, Myanmar, China, Japan, and the Philippines, and from seven locations in Micronesia, Melanesia and Polynesia. Varying levels of resistance to TLB were noted [82]. Interestingly, 40% of 424 indigenous accessions at the Central Tuber Crop Research Institute of India were reported to show tolerance to TLB [83].

7.4. Breeding for Resistance to Taro Leaf Blight

Taro leaf blight control by breeding for resistance has proven to be an extremely cost-effective and environmentally acceptable approach [34,84–86]. The success of breeding for resistance against TLB depends on the availability of genetic resources and the type of resistance they confer [74,87]. The use of polygenic or HR is one of the most effective means to control TLB [8,86]. This breeding strategy involves the systematic selection of the resistant individuals from a population followed by recombination of the selected individuals to form a new population (recurrent selection). The main

advantage of this strategy is its ability to accumulate minor resistance genes, which individually would confer minimal resistance [86], but together are likely to be additive and provide durable disease resistance. Because HR is not pathotype specific, failure to identify different pathotypes is not a limiting factor to the strategy [70,86]. A major challenge however, is the reliable identification of the least susceptible individuals in the population for use in the next cycle of inter-crossing. With HR breeding strategies, it is normal to generate many progenies of good agronomic quality differing widely in their degree of disease resistance. Such a range of material provides the opportunity to match the degree of resistance to the potential risk of disease [53]. Taro breeding programs have been implemented at a number of institutes worldwide, with those in Hawaii, Papua New Guinea, Samoa and Solomon Islands specifically focused on TLB.

The Papua New Guinea taro breeding program is based on a modified recurrent selection strategy and gives high priority to TLB resistance. Cycle-1 was developed in 1994 by crossing the resistant base population with superior (high yielding and tasting) local taro varieties [88]. Some partially superior genotypes were recovered from cycle-1 from among a majority that retained undesirable wild characteristics. Cycle-2 was created in 1996 by inter-crossing these partially superior genotypes. Three new varieties (NT 01, NT 02 and NT 03) were released from cycle-2 in 2001 [86,89], and one variety (NT 04) was released from cycle-3 by inter-crossing selected cycle-2 genotypes [8]. The development of these high-yielding varieties of taro has helped to reduce the threat of TLB in Papua New Guinea. The varieties performed well in farmers' fields giving over 50% higher yields (about 9 t/ha) than the popular variety "Numkowec" (about 6 t/ha) used as a check [89]. These breeders' lines have been widely adopted in many areas of Papua New Guinea [90]. Other elite hybrids (with high yield, acceptable palatability and resistance to TLB) have been identified post cycle-3 and are being considered for official release.

It is likely that those lines released from advanced cycles will be superior in their attributes, especially palatability, because of the polygenic breeding approach (accumulation of superior genes from cycle to cycle) adopted by the Papua New Guinea program. It appears from recent analyses that breeding selections have reached a plateau in terms of yield, and to make further genetic gains there is a need to cross local varieties with taro of different genetic backgrounds [91].

The goal of the Hawaii taro breeding program is to improve commercial taro for pest resistance, including TLB, and to increase genetic diversity. At the earlier stages of the program, a single source of TLB resistance from Palau was crossed with Hawaiian taro [68,92]. Later, multiple sources of resistance were introduced from Micronesia, Palau, Indonesia, Papua New Guinea, Thailand and Nepal. In cycle-1, crosses were made between commercial cultivars and introduced genotypes. The resulting hybrids were evaluated for desirable agronomic traits, and elite hybrids selected for the next cycle. The breeding program is based on two approaches. The first approach is similar to the breeding program in Papua New Guinea, and involves crossing commercial taro with TLB-resistant wild varieties from Thailand and Papua New Guinea. In this process, additional breeding (modified backcrossing or rigid selection through an extra generation) is needed to produce elite hybrids. This requires at least four years. The second approach is to cross commercial taro with TLB-resistant taro from Palau and Micronesia. In this process, elite types can be selected in the first year. Several new hybrids were produced including hybrids "99-6," "99-7," and "99-9". These hybrids have greater

tolerance to TLB, and yield 30% more than the industry standards, to which they are comparable in corn taste and colour [93].

The Samoan taro breeding program is different from that in Papua New Guinea and Hawaii. A participatory approach to breeding was adopted from the outset, which involved researchers, farmers and extension staff [29]. The Taro Improvement Program (TIP) at the University of the South Pacific began in early 1999. The aim was to bring together taro farmers via crop-focused participatory appraisals and provide them with options for improving production and managing TLB [29]. TIP made good progress and farmers evaluated and selected clones derived from crosses between local (Samoan) cultivars and those from Palau and the Federated States of Micronesia [29]. Later, to broaden the genetic diversity of the breeders' lines, the program has made crosses using varieties from Asia to improve further TLB resistance whilst retaining the quality characteristics favoured by Samoans and the export market in New Zealand. To date, seven cycles of breeding have been completed. In 2009, the Ministry of Agriculture in Samoa released five TLB-resistant cultivars of which Samoa 1 and 2, identified from breeding cycle-5, are the most preferred for export [94,95].

The Vanuatu breeding program is based on combining genotypes from the two major gene pools to establish a wide genetic base [96]. Elite cultivars for desired agronomic characteristics have been identified, based on an eco-geographic survey of the genetic variation existing in the region and systematic characterisation using morphological, agronomic and molecular characters. The resultant selections have been exchanged between participating countries: the Philippines, Vietnam, Thailand, Malaysia, Indonesia, Papua New Guinea and Vanuatu [79,97].

8. Role of Regional Networks for Controlling Taro Leaf Blight

After the serious outbreak of disease in Samoa in 1993, the occurrence of periodic epidemics in Papua New Guinea and Solomon Islands, and the threat of introduction of TLB to disease-free countries, the Pacific islands sought a regional collaborative approach to deal with the problem. No one country has sufficient resources to tackle the problem alone. There is much to be gained by countries participating in a regional network which facilitates germplasm sharing and enhancement, and keeps countries informed of activities in the region and outside. This provides a mechanism whereby collaboration can be fostered to achieve a more strategic approach to TLB control and taro improvement generally. It was identified that major constraints for taro breeding programs including TLB resistance breeding are the lack of knowledge of the genetic diversity in the cultivars, the limitations in access to and knowledge of additional sources of disease resistance as well as the absence of information on the potential agronomic and processing value of genotypes [74].

The crop network model was conceptualized with implementation of two regional collaborative projects. The first network, the AusAID-funded Taro Genetic Resources: Conservation and Utilization Network (TaroGen) re-activated the Papua New Guinea and Samoan TLB resistance breeding programs after a long dormant period, and linked them closely with other Pacific programs for the development of a core collection for Pacific taro and the safe sharing of virus-indexed breeders' lines and traditional cultivars [86]. To link the Pacific with South-east Asia, a second network, the EU-funded Taro Network for South-east Asia and Oceania (TANSOA) was established [98]. Through

the collaborative research that developed, there were notable achievements, and in less than a decade high yielding progenies resistant to TLB were developed.

Both TaroGen and TANSOA established networks incorporating local universities and research institutions, with regional and international organizations. Under TaroGen national collections (more than 2000 accessions) were assembled, characterized to identify a regional core representing the genetic diversity of taro in the region, and conserved [80,99]. Under TANSOA, a core sample was made that captured much of the genetic diversity from South-east Asia. Both networks successfully improved taro quality and resistance to TLB. They also achieved significant outputs in diagnostics for taro viruses, as well as initiated the establishment of regional genebanks in Fiji (SPC) and Indonesia (LIPI). The SPC genebank is now an international hub for the conservation and distribution of taro in Asia and the Pacific.

The success of these two networks laid the foundation for the genesis of a new initiative, the International Network for Edible Aroids (INEA) which aims to link all the major taro genepools and promote the interchange of taro genetic resources worldwide (www.ediblearoids.org) [100]. In addition to many food security goals, this new network holds the potential to manage TLB, especially in West Africa where extensive epidemics have been reported recently.

9. Way Forward for Mitigating Impact of TLB on Food Security

Taro leaf blight has been a particularly destructive disease in the Pacific and South-east Asia over many decades and has now reached West Africa. Food security of smallholder farmers has been threatened in all these regions, and in some cases economies put at risk, as the disease is difficult to manage by conventional means. The only solution has come through resistance breeding, but the difficulty in this approach has been a lack of a worldwide coordinated strategy. However, in recent years the success of regional interventions has given hope and shown that collaboration between countries is possible and has great merit. This success has largely come from the result of the networks built under TaroGen and TANSOA [91]. Genetic resources were collected and shared and used to breed for resistance. The key lessons learnt from TaroGen and TANSOA collaboration were: the need to use modern biotechnologies to solve crop improvement problems, linking countries, regional institutions and universities with centres of excellence outside the regions that specialise in DNA fingerprinting, virus indexing and conservation; that farmers must be involved in taro breeding from the outset; and that effective and efficient project co-ordination is required, ensuring interaction among national programs, other partners and funding agencies [101]. These are the strategies now being implemented by INEA to use taro and other edible aroids to build a model to improve clonally propagated crops of the tropics. INEA is a timely intervention, coming at a critical time for farmers in West Africa who are now suffering the consequences from the inadvertent introduction of TLB to that continent. The devastation caused there is a salient reminder of the potential of *P. colocasiae* to undermine food security and the need for lasting solutions.

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